12.—A CONSIDERATION OF THE INSECT POPULATION ASSOCIATED WITH COW DUNG AT CRAWLEY, W.A.

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1. INTRODUCTION.

The research work described in this paper is an attempt to indicate the main insects which form the population of cow dung at Crawley and to assign them to their proper place in the ecology of that substance. Most of the work was performed at the Biology Department, Crawley, during the periods February to November, 1940, and February, 1941, to February, 1942. Two cows supplied most of the dung utilised, but supporting observations at Maylands and Spearwood showed that this restricted amount of material indicated correctly the qualitative nature of the population, a conclusion borne out by the study of insects in the dung dropped by a herd of fifteen cows grazing in the grounds of the University. The writer also had the opportunity of examining cow dung from Armadale, and in August, 1941, was able to pay a visit to Katanning to make a rapid comparative survey of the cow dung population.

Katanning (latitude 33° 38′ S., longitude 117° 35′ E.) has a climate of the continental type, characterised by a considerable variation between maximum and minimum temperatures. Perth (latitude 31° 52′ S, longitude 116° 3′ E.) has a Mediterranean climate with less difference between the extremes of temperature. The rainfall at Katanning, although annually amounting to only about half that at Perth, is much more evenly distributed throughout the year, rainfall at Perth being essentially of the winter type.

Table 1.

The mean daily maximum and minimum temperatures, the mean daily relative humidity, and the mean annual rainfall at Katanning and Perth, Western Australia, for 34 years prior to 1932 (based on figures from the Weather Bureau, Perth):—

	PERTH.	KATANNING.
Maximum °C.	22·89	21·94
Minimum °C.	12·89	9·11
Humidity (%)	63	70
Rainfall (inches)	34·7	18·7

2. METHODS.

No accurate quantitative work was attempted in this general approach to the problem. The insects found in various cow dungs were submitted to experts for identification where possible and observations made on their habits. Portions of cow dung containing immature stages were brought into the laboratory for study of phases of the life histories of the insects concerned.

3. SUCCESSION.

A large number of insect species are associated with faecal matter, especially with that of mammals, which is usually of sufficient quantity to form an ecological habitat of some duration.

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In an unstable environment of a restricted nature, of which cow dung is an example, two main factors operate to influence the type of population present at any particular time. Firstly, the external climatic conditions change the nature of the environment, thus making it less suitable for the species which occupies it first. Secondly, the animals themselves, principally by interspecific competition, to a lesser extent by altering the physical and chemical nature of their environment, tend to bring about an alteration in the type of population. Ultimately a stage is reached at which a primary species is displaced by one more adapted to the changed conditions. The process continues until the environment is destroyed. This termination of the succession by destruction of the environment, which is characteristic of the animal ecology, serves to balance, in the broad cycle of energy of nature, the synthetic tendencies of plant successions in which a stable association is finally attained (Chapman, 1931).

The phenomenon of succession has received most attention from plant ecologists. The most clear cut examples of succession in animal ecology are found in certain restricted environments. The work of Graham (1925) on the succession of animals in a felled tree trunk may be cited here. He concluded that there was a definite succession of organisms as the chemical and physical characters of the wood changed during the process of decay and disintegration. Fuller (1934) found this statement to be equally true of the population of a carcass.

In the case of cow dung, the succession is not clear cut and only detailed study would reveal the causes of some apparent anomalies. The nature of the succession will be discussed after the insects concerned have been dealt with.

4. THE CHANGES IN COW DUNG AFTER DROPPING.

The initial nature of a cow dung varies considerably with the diet of the animal. The dung of a grass-fed cow differs from that of one fed on dried feed in its green colour, soft texture, and the subsequent course of its disintegration. The process of decay can be arbitrarily divided into five stages, of which the first three differ markedly from the last two. A characteristic insect population occupies the first three stages and a different one succeeds it in the last two. Certain distinctions can in many cases be drawn between the populations of Stages 1, 2, and 3, but equally often they are almost identical.

Following is the typical course of changes in dung from a grass-fed cow :—

1st Stage.

When dropped, the dung is green or more rarely tan in colour, semiliquid, and with a noticeable odour. Cow dung is characteristically a " cold " dung and high temperatures due to fermentation are unusual, especially in isolated cakes, although the temperature of the dung during the day may be high owing to exposure to the sun (Davidson, 1937). The slight degree of fermentation undoubtedly influences the insect population since certain insects, *e.g.*, the house fly, are specifically attracted to fermentable materials either by high temperatures or products of such decomposition.

The first obvious change in the cow dung is the formation of a thin blackish skin over the exposed surface of the soft mass. By evaporation of moisture, this skin ultimately becomes a thick, firm crust pierced by many cracks which expose the softer interior. The superficial skin is the result of an oxidation process dependent on free access of atmospheric oxygen, since it does not form on artificially covered cakes or those which for any reason are kept exceedingly moist.

2nd Stage.

The colour changes from tan or green to a light brown shade. The whole cake becomes firmer as a result of evaporation of moisture. The odour is still noticeable even when the surface remains unbroken.

3rd Stage.

The dung becomes blacker and firmer in texture. The fibres of the undigested food can be distinguished, because evaporation of moisture has concentrated the suspension of which they form the discontinuous phase. The odour is usually not noticeable unless the surface of the dung is disturbed.

4th Stage.

Evaporation of moisture has proceeded to the extent that undigested food fibres interlock to form a matrix firm enough for the whole cake to be held by the edge without breaking. The internal colour is a dull rusty brown. The surfaco layers of the dung are completely dry and of a bleached brown or even white colour due to the precipitation of salts.

5th Stage.

The entire dung becomes of the same nature as the upper portions of a fourth stage dung. It is firm, bleached brown, in some cases almost white, dry, hard, and noticeably light for its volume. In the later part of this stage no insects except casual shelterers are present.

A number of variations from the above cycle are possible. All parts of a dung cake do not necessarily pass through the same stage at the same time. For instance, dungs which have the upper layers in the fourth, and lower portions in the second or third stage, are common. Further, the changes in colour, texture, and moisture do not always proceed at the same rate. Dungs sometimes preserve the initial green colour although in other respects they could be classed as in the fourth stage. Such peculiarities are due to some unusual feature in the history of the cake, such as freedom from invasion by insects or conditions which artificially preserve the moisture content.

An important departure from the cycle outlined above is the omission of either the second or the third stage. The colour of a dung may pass straight from green to black, *i.e.*, direct from first to third, or from light brown to dark brown, *i.e.*, from second to fourth. In such cases, the population of the omitted stage is found in the early part of the third or late part of the second according to whether the second or third has been reduced.

In the field, large numbers of dungs disintegrate before they reach the fifth stage, an occurrence very frequent during the height of the summer.

The time taken to pass through the various stages of decomposition varies greatly with climatic conditions, so that, except within wide limits, the absolute age of the dung has little significance. High temperatures speed up the process of disintegration by accelerating the chemical and physical processes within the dung and by stimulating the contained insects. Rain has the reverse effect, and the stages of a dung exposed to rain may be indefinitely prolonged.

The following table indicates a few variations in absolute time of stage duration for various conditions of rainfall and temperature :—

Table 2.

Duration in days of each separate stage numbered.

Date of Dropping.	1.	2.	3.	4.	5.	Rain during period of disintegration.	Temperature during period of disintegration.
20–3–41 ...	$\frac{18}{24}$	‡	$1\frac{3}{4}$	7	*	*Nil*	20·6° C.
2–4–41 ...	2	‡	8	15	*	2·84″	18·0° C.
7–4–41 ...	1	‡	$3\frac{1}{2}$	10	*	1·50″	17·6° C.
31–5–41 ...	4	8	14	*	...	7·07″	14·2° C.
4–6–41 ...	8	7	29	40	*	20·00″	13·9° C.
12–6–41 ...	9	†23	...	41	*	17·14″	13·9° C.
22–6–41 ...	7	18	*	...	...	5·52″	14·2° C.
23–7–41 ...	8	3	29	*	...	6·86″	13·9° C.

* Broken up in this stage. † 23 Duration of stage 2 plus 3 because they could not be separated. ‡ Omitted.

Insects are rarely responsible for the complete destruction of a cow dung, this being accomplished by rain and other mechanical agencies. On the other hand, cakes may remain in the fifth stage for years without noticeable erosion.

The cycle in a dung heap is substantially the same as that in a single cake, although the duration of the stages is usually greater because the inner portions are less accessible to disruptive influences.

5. THE INSECTS CONCERNED.

The following is a list of the Insect Species associated with cow dung at Crawley, Western Australia :—

Collembola
- F : Hypogastruridae
  - * Unidentified specimens

Dermaptera
- F : Labiduridae
  - Unidentified species

Orthoptera
- F : Tettigoniidae
  - Unidentified specimens
- F : Gryllotalpidae
  - Cylindracheta sp.

Hemiptera
- F : Pentatomidae
  - Unidentified specimens
- F : Coccidae
  - Unidentified specimens

Coleoptera
- F : Carabidae
  - Promecoderus albanyensis, Cast.
- F : Hydrophilidae
  - * Cercyon haemorrhoidalis, Fab.
  - * Cercyon nigriceps, Marsh.
  - ? Paracymus sp.
- F : Staphylinidae
  - Creophilus erythrocephalus, Fab.
  - * Cryptobium elegans, Blkb.
  - * Leptacinus socius, Fauv.
  - Philonthus sp.
  - Oxytelus spp.
- F : Silphidae
  - ? Choleva sp.
- F : Trichopterygidae
  - ? Epoptia sp.
  - ? Philagarica sp.
- F : Histeridae
  - Saprinus incisus, Er.
  - Saprinus spp.
  - Hister walkeri, Lea.
  - Platysoma ? multistriatum, Lea.
- F : Nitidulidae
  - Carpophilus hemipterus, Linn.
  - ? Brachypeplus sp.
- F : Colydiidae
  - Pabula dentata, Blkb.
- F : Ptinidae
  - ? Ptinus sp.

* Breeding in cow dung.

F : Scarabacidae
* Aphodius lividus, Oliv.
Aphodius insignior, Blkb.
Aphodius grauarius, Linn.
Aphodius ambiguus, Boh.
Aphodius sp.
* Proctophanes sculptus, Hope.
Ataenius ? integricollis, Lea.
Onthophagus ferox, Har.

F : Anthicidae
Anthicus hesperi, King.

F : Tenebrionidae
Gonocephalum arenarium, Fab.
Adelium scytallicum, Pasc.

Diptera
F : Psychodidae
* ? Psychoda spp.

F : Sciaridae
* Sciara spp
* ? Zygoneura sp.

F : Scatopsidae
? Rhegmoclema sp.

F : Mycetophilidae
? Mycetophila sp.

F : Tipulidae
Eriopterinae
* Unidentified species

F : Stratiomyidae
Neoexaireta spinigera, Wied.

F : Dolichopodidae
? Asyndetus sp.

F : Phoridae
? Chaetocnemistoptera sp.

F : Sepsidae
* Sepsis plebeia, de Meij.
* Australosepsis fulvescens, Mall.
* Australosepsis fulvescens var. atratula, Mall.

F : Borboridae
* Leptocera spp.

F : Drosophilidae
* ? Cladochaeta sp.

F : Otitidae
* Chrysomyza aenea, Fab.
Pogonortalis barbifera, Macq.

F : Calliphoridae
Calliphorinae
Calliphora (Neopollenia) australis, Boisd.
Calliphora (Proeckon) nociva, Hardy.
Lucilia cuprina, Wied.
Sarcophaginae
* Sarcophaga (Parasarcophaga) depressa, Desvoidy

F : Muscidae
Muscinae
* Musca vetustissima, Walker.
* Musca domestica, Linn.
Anthomyiinae
* Hylemyia deceptiva, Mall. or near
* Hylemyia sp.
Fanniinae
* ? Fannia sp.

Phaoniinae
* Helina hypopleuralis, Mall. or near
* Helina coerulescens, Stein.
* Helina regina, Mal. or near
* Rhynchomydaea (Hardyia) carinata, Stein or near
* Muscina stabulans, Meig.

Lepidoptera
F : Oecophoridae
* Unidentified species

Hymenoptera
F : Alysiidae
1 unidentified species

F : Figitidae
1 unidentified species

F3 : Formicidae
Unidentified species

6. RELATIONS OF INSECTS TO THEIR ENVIRONMENT AND TO EACH OTHER.

These may be outlined as follows :—

1. Those which do not live in the cake itself but use it as food, *e.g.*, blowflies, Coprine beetles.

2. Predators on dung insects with no closer relationship to the dung. These usually remain on the outside of the cake, *e.g.*, Dolichopodids, *Creophilus erythrocephalus*, and ants.

3. Those which live in or on the dung, but subsist on the fungal growths which it supports. Probably the minute Collembola frequenting dung have this habit, although their small size renders the elucidation of this point very difficult.

4. Insects, the larval stages of which live in and feed upon dung while the adults have other feeding habits, *e.g.*, some Sarcophagids and probably *Neoexaireta spinigera*.

5. Insects which are predatory themselves or have predatory larvae and of which the whole life history is passed within the dung, *e.g.*, *Oxytelus*, *Leptacinus*, *Cryptobium*, *Saprinus*, and *Platysoma*.

* Reared from cow dung.

6. Insects which use the dung as a shelter, *e.g.*, Pentatomida, Dermaptera, and Tenebrionids, the association of which with the rest of the cow dung population is only of the most casual nature. Ants are in this class but they are also predatory.
7. The true dung insects, which are coprophagous and pass through their entire life history in the dung, *e.g.*, the Aphodii. Owing to a doubt concerning the food of the larvae of the Cercyons, it is not known whether they can be classed here.
8. Parasites of dung-living larvae, *e.g.*, Alysiids and Figitids.

7. NOTES ON THE INSECTS ASSOCIATED WITH COW DUNG AT CRAWLEY.

Order 1—COLLEMBOLA.

Myriads of minute blue insects belonging to the Hypogastruridae occur in and on dung during the winter, June to August. Large numbers occur in any stage of the dung providing it has remained fairly moist.

The whole life history can apparently be passed through in cow dung. Eggs are fairly common in the dung, most noticeably so in June. Some brought into the laboratory in June, 1941, hatched in twelve days, but the insects were not raised to maturity. At times, parts of first and second stage dungs in the field are almost white with the exuviae of these tiny insects.

Order 2—DERMAPTERA.

Unidentified specimens of Labiduroid Dermaptera are occasionally shelterers under cow dungs in the field. The association with the dung appears to be nothing more than casual.

Order 3—ORTHOPTERA.

Tettigoniid nymphs are sometimes found sheltering under old cow dung, while a *Cylindracheta* species found at Crawley is apparently capable of a truly coprophagous habit, since two specimens lived for some weeks on a diet of pure cow dung.

Order 4—HEMIPTERA.

At Katanning in August, 1941, a number of Pentatomids were collected in crevices of very old fifth stage dungs which they used as a shelter only. The same is true of Coccid nymphs found under old dungs at Spearwood, Western Australia, in April, 1941.

Order 5—COLEOPTERA.

F. 1. **CARABIDAE.**

Promecoderus albanyensis, Cast.

Specimens of this wingless beetle occur under cow dung at Crawley. It is presumably predaceous but its timidity has so far prevented observation of its habits.

The larvae of unidentified Carabs are also common under, and more rarely in, dung cakes. One was kept alive during August and September, 1941, on a diet of Sepsid and Sciarid larvae, but died before pupating.

F. 2. **HYDROPHILIDAE.**

The genus *Cercyon* contains both aquatic and terrestrial species, many of the latter being inhabitants of dung, Stephens (1839) having described

42 species with this habit. *Sphaeridium*, a coprophagous genus which I have not seen recorded from Australia, is associated with *Cercyon* in both England and France, especially in cow dung (Lacordaire, 1854), and in Ceylon and Japan aquatic species of both occur (Sharp, 1884, 1890).

Cercyon haemorrhoidalis, Fab.

This introduced species is represented at both Crawley and Katanning by two easily separated varieties. One is most numerous between November and June (Pl. 1, Fig. 1), the other between June and November, both being present all the year round. The species occurs also in carrion, decaying grass, and horse manure.

With the Aphodiines, Staphylinids, and Histerids, they arrive at the dung soon after dropping, the odour being apparently the attracting stimulus. At first they congregate on the under surface or in the natural cracks of the dung. From these vantage points the work of penetration begins. The adults are coprophagous, and tunnelled out dung is eaten, since no waste is found outside infested cakes. The area of penetration is peripheral at first, then the insects concentrate on the upper surface. Many dungs are found with an almost unaltered core, though the superficial layers are completely penetrated underneath the firm outer crust which is pierced by numerous holes.

Under favourable conditions of fine days and high temperatures cakes may be riddled into a bran-like mass in a single day. Where heavy rain has fallen or low temperatures prevail, the process of penetration may be greatly slowed down, and may not even occur to any extent at all.

The specimens of *Cercyon haemorrhoidalis* run into dark places only when a dung is disturbed, and are otherwise tolerant of light.

The beetles leave the dung after a varying period, which is generally from four to fourteen days. It may be much longer and fluctuates considerably from cake to cake under identical external conditions. During this period, which is one of trophic activity, eggs are deposited, since larvae begin to appear in the third stage dung. I have not been able to isolate the eggs of the species in spite of the larvae being fairly plentiful. Numbers of females caged with dung in the laboratory died without oviposition, yet dissection showed their ovaries contained numerous oocytes.

Exactly what the legless mandibulate larva (Pl. 1, Fig. 2) feeds on is a problem. The gut contains a translucent reddish-brown liquid full of oil globules which cannot certainly be recognised as a derivative of cow dung. Development occupies approximately 10 to 14 days in pure cow dung.

Pupation generally occurs in the dung itself in a small cavity excavated by the prepupa near to the outer surface. Where the dung has remained very moist, pupation may occur in the sand below the dung. No cocoon of any sort is formed. The pupae are of the usual exarate coleopterous type and, like many other white or yellow immature stages of insects, is negatively phototropic.

The pupal period was observed to range from three days in April (18° C.) to 11 days in September (13·9° C.). The life cycle from egg to adult took less than 29 days at temperatures from 13·9° C. to 16·1° C. in September and October, 1941.

There is an indefinite number of generations per year, as larvae and pupae occur in numbers at Crawley for most of the year except for a marked pause in June and July, when only occasional ones are found. Owing to the comparatively short duration of stages suitable to *Cercyon* larvae, a second generation never develops in any one dung cake.

Cercyon nigriceps, Marsh.

This small species is associated with C. haemorrhoidalis at Crawley and Katanning, though always in small numbers. Its life history and habits are similar to those of its larger relation.

? Paracymus, sp.

A number of small beetles taken in cow dung at Crawley in April, 1941, probably belong to this genus. Their rarity indicates that they are of little importance in the dung community.

F. 3. **STAPHYLINIDAE.**

Creophilus erythrocephalus, Fab.

On warm days at most times of the year specimens of this beetle gather on fresh dung cakes to catch Sepsids and Borborids attracted to it. Usually they remain on the outside of the cake, but may retreat into cracks if disturbed, or even hollow out cavities on its lower surface. According to Fuller (1934) they attack immature stages of sheep blowflies breeding in carrion, without appearing in sufficient numbers to have much effect on the maggot population of a carcass. This is also true of the dung cake, as rarely more than six specimens will be found on the one pad, which means that only a small percentage of the myriads of flies which foregather are destroyed. *C. erythrocephalus* rarely remains after the decline in number of flies consequent on the formation of a superficial crust on the cake. Because of this it is not known whether it will attack dung-inhabiting larvae.

Philonthus, sp.

An unidentified species of this genus is occasionally found in small numbers, usually in second or third stage cow dung. It is more numerous in decaying grass. Fuller (1934) states that *P. Politus*, Linn. eats eggs and young larval blowflies in carrion. The genus is common in England, where four species are recorded by Stephens (1939), mostly in dung, and it is represented in New Zealand (Broun, 1880).

Leptacinus socius, Fauv.

This species, which is presumably predaceous on small Dipterous larvae, is present in numbers less than the Cercyons throughout the year in cow dung of all stages, mainly in the first and third. It was not seen at Katanning in August, 1941. Although Staphylinid eggs and larvae are common in fourth stage dung, attempts to obtain adults failed. The larvae of *Leptacinus socius* may leave the dung to pupate because in September, 1941, pupae were found in the sand under an 81 day old dung kept in the laboratory since dropping. Dung from Armadale collected in March, 1941, contained a pupa (Pl, 1, Fig. 3) of this beetle actually in the dung itself.

The pupal period under laboratory conditions was found to be in the region of 26 days at an average temperature of 13·9° C. in September, 1941.

Cryptobium elegans, Bikb.

This species is associated with *L. socius*, but nothing of its life history is known. The genus is represented by 20 species in England, 19 of which live in dung and similar material (Stephens, 1839).

Oxytelus, sp.

Several unidentified species are numerous in cow dung, sometimes greatly exceeding *Leptacinus* and *Cryptobium* in numbers. They are among the first to colonise freshly dropped dung, especially if it has been scattered in a number of shallow pieces. They also occur in numbers in carrion. In northern Australia they may play a part in reducing the incidence of the Buffalo Fly (*Lyperosia exigua*, de Meij) by competing with its larvae in cow dung (Mackerass, 1932).

The only immature stage seen was a single exarate pupa in September, 1941, in the sand under dung, three months old, kept in the laboratory since dropping.

F. 4. SILPHIDAE.

Only two specimens, probably belonging to *Choleva* sp., were collected from third stage cow dung at Crawley in March, 1941, and hence the family is unimportant in the succession. Two species of *Choleva* occur in carrion (Fuller, 1934).

F. 5. TRICHOPTERYGIDAE.

At Crawley, species near *Epoptia* and *Philagarica* in cow dung in all stages, especially in the fourth if it is not too dry. Their habits are not known. The family is best represented in the tropics, occurring in rubbish, leaves, under bark or in rotten wood (Lefroy, 1923).

F. 6. HISTERIDAE.

Members of this family are present in cow dung at Crawley between October and May, although they are found in carrion and decaying grass at other seasons of the year.

SAPRINUS.

Two species of this genus occur in cow dung of which only one, *S. incisus* Er., has been identified. Both exhibit a preference for fresh cow dung and tolerate excess moisture better than do the Hydrophilids.

They never remain in the dung beyond the third stage, which is the one containing the majority of their prey, larvae of Sepsids, Drosophilids, and probably Borborids. Small quantities of dung are also eaten. Three larvae were found in fourth stage dung brought from Armadale to St. George's College in March, 1941. One of these subsequently pupated ; the adult emerging after three weeks at an average temperature of 18° C.

The genus *Saprinus*, like other insects in decaying materials, is widespread. Species of it occur in England (Stephens, 1839), New Zealand (Broun, 1880), and in carrion at Canberra (Fuller, 1934).

PLATYSOMA.

One specimen of *P. ? multistriatum*, Lea, was collected in second stage cow dung on 4th March, 1941. Stephens (1839) describes three species in England all under bark.

HISTER.

H. walkeri, Lew., is the largest of the dung-frequenting beetles at Crawley. It is most numerous from October to April. It is frequently found in quiescent state in the moist sand below a cake and is not often found inside. In this it differs from *H. coenosus*, which in Haiti is such an efficient predator on Museoid maggots in fresh moist dung that Myers (1938) has recommended its introduction into Australia as a possible control of the Buffalo Fly.

The local species is also predatory on maggots. It probably takes up its characteristic position in order to catch maggots which come to pupate on the lower surface of the cake. Unlike *Saprinus*, it may occur with fourth stage dung.

Hister is represented in England and New Zealand.

F. 7. NITIDULIDAE.

One specimen of *Carpophilus hemipterus*, Linn., which in California is an important pest of fresh and dried figs (Simmons, Reed, McGregor, 1931), was collected from second stage dung in September, 1940. If due to anything but chance, its presence indicates a considerable departure from the usual habits of the species. In April, 1940, two specimens of *? Brachypeplus* sp. were also found in dung of the same stage.

F. 8. COLYDIIDAE.

Three specimens of *Pabula dentata* Blkb. were obtained from cow dung in April, 1941. The members of the family are generally found in leaf mould, decaying wood or under bark (Tillyard, 1926).

F. 9. PTINIDAE.

In May, 1941, a single specimen of ? *Ptinus* sp. was found in a dry, bleached fifth-stage pad. Its presence, if not merely fortuitous, adds yet another food material to the remarkable list given for the family by Esdaile (1927)—farinaceous matter, drugs, books, tobacco, spices, pepper, and wood.

F. 10. SCARABAEIDAE.

APHODIUS.

Aphodius lividus Oliv.

This species has a world-wide distribution (Schmidt, 1922). With *Ataenius stercorator* it is abundant in Puerto Rico, where the two eat so much of the fresh cow dung that the larvae of the Horn Fly (*Lyperosia irritans*) can scarcely live. (Observations quoted by Myers, 1938). Myers, however, states that in Haiti these beetles have little effect on the population density of the Horn Fly. *A. lividus* occurs in large numbers at Uvalde, Texas, U.S.A., where 1,113 specimens have been collected from a single dropping (Lindquist, 1935). Though not yet finalised, sampling counts at Crawley indicate that greater numbers per cake are not unusual here. Stephens (1839) includes it in his list of fifty-seven English species of *Aphodius*, nearly all of which occur in dung. Boucomont (1929) reports its presence in dung in China. At Crawley it forms a prominent part of the population of both horse and cow dung and is present at Katanning. At Crawley it appears at and enters the dung shortly after dropping, leaving again at some time in the third stage. All feeding stages are coprophagous.

The actual information on the life history of *A. lividus* is slight and much of it must be conjectured. This is due to the slow growth of the larvae and the difficulty of handling them under laboratory conditions. Eggs and larvae of Scarabs are numerous in cow dung at Crawley, but strangely enough most of them are those of *Proctophanes sculptus* Hope, the adults of which are much fewer in number than those of *A. lividus*.

Scarab eggs are common in fourth stage dung from February to August. Eggs have been kept in the laboratory up to 11 days before hatching. This represents less than the minimum egg period since none were actually collected immediately after laying. Although Scarab larvae are adapted to the firm, rusty-brown dung of the fourth stage, they sometimes occur in the moister, fresher dung of the third.

The life history period from the egg to the emergence of the adult was found to be as short as 45 days during March (average temperature 20·6° C.) and April (18·6° C.), 1941. Three larvae which pupated in April emerged in May after pupal periods of fourteen to sixteen days. It seems that under certain circumstances the period of development from the egg to the adult can be considerably shorter than that of *A. tasmaniae*, which is approximately one year (Swan, 1934). Lindquist (1935) estimated the life history period of *A. lividus* to be 25 to 45 days at Uvalde, U.S.A. under laboratory conditions.

Pupation usually occurs in the sand below the dung., the pupa (Pl. 1, Fig. 4) being unprotected by any cocoon structure.

It is probable that the species breeds in other media besides cow dung, since the larvae seen were very few compared with the large number of adults.

Aphodius insignior, Blkb.

Blackburn (1904) erected this species from specimens taken near the Swan River, and Schmidt (1922) only gives Western Australia as its area of distribution.

No representatives were found at Katanning in August, 1941. At Crawley they show a remarkable seasonal distribution. Up till June, 4, 1941, no specimens had been collected since August, 1940. On that date one specimen was discovered in a second stage cow dung. On 16th June, following rain, myriads appeared, swarming in fresh dung near the Biology Department. They practically excluded all other beetles and burrowed even into the most liquid cakes. The large numbers were maintained until the end of July when a decline set in. By 30th August they had again disappeared.

This appearance in large numbers suggests that *A. insignior* has a life history similar to that of *A. tasmaniae*, which has an annual emergence of adults over a short period of the year. As no immature stages of *A. insignior* have so far been found, this must remain conjectural for the present.

The species exhibits a marked preference for fresh, greenish dung on which it feeds freely. The beetles are exceedingly tolerant of moist conditions, which gives them a considerable advantage over other insects in colonising cakes. When inside the dung or on it they habitually associate in pairs. Hanging on to the prothorax of the female with its forelegs, the male is carried round on her back and requires considerable persuasion to dismount. This habit is no doubt a prelude to mating, though actual copulation has not been observed.

A. insignior rarely remains on the dung beyond the second stage.

Aphodius granarius, Linn.

This world-wide species is present both at Crawley and Katanning in horse and cow dung. Its small numbers preclude its being of much importance in the succession.

Aphodius ambiguus, Bohem.

Also known as *A. frenchi* Blkb, this species is widely distributed in Africa and Australia (Lea, 1923). Its importance in the dung community varies greatly at Crawley and Katanning. At Crawley, specimens are most numerous in the period May to August, the total range being from mid-April to October. Their numbers are always far short of those of *A. lividus* or *C. haemorrhoidalis*. They appear beneath the fresh dung, where they remain until the majority of the other dung-invading beetles have left. By this time the dung has usually attained the fourth stage. The beetles then commence to migrate inside. This well marked succession of the species to the others is a feature of the winter cycle in dung. In many cases they remain quiescent on the lower surface without entering the dung. While they have never been seen feeding, the gut contents indicate that dung forms the staple food. At Crawley they also frequent rotting bark, carrion, and decaying grass.

At Katanning in August, 1941, a different state of affairs was seen. Instead of being in the minority, they far exceeded all the other dung-frequenting beetles in number. As at Crawley, they tended to remain on the lower surface of cakes of all stages though numbers had penetrated even into fresh dung.

Nothing is known of the life history of *A. ambiguus* in spite of the presence of numerous females with well-developed oocytes in their ovaries. Possibly some of the Scarab larvae found in the cow dung belong to this species.

Proctophanes sculptus, Hope.

This bulky beetle occurs all the year round at Crawley, becoming most numerous in the period May to August. Its position in the succession is difficult to estimate as it frequently occurs associated with *A. ambiguus* but also singly in very fresh and more rarely in dry fifth stage dung. Both larvae and adults are coprophagous.

Owing to the length of the life history and the fierce competition offered by Scarid larvae under laboratory conditions, the information on it has been collected only from a few cases. Seven specimens were reared from the egg during the period June to November, 1941, and the length of the period from hatching to emergence of the adult ranged from 97 to 157 days.

The eggs, which are scattered singly in fourth stage dung, hatch about 12 days after laying. The pupal period is approximately three weeks, the pupae being found in the sand under the dung. The larval period is thus shorter than that of *Aphodius tasmaniae* (Swan, 1934), which takes from April to December. The larvae *Proctophanes* may remain in a quiescent non-feeding state for as long as 48 days prior to pupation.

Ataenius ? integricollis, Lea.

In August, 1940, three specimens were collected in cow dung at Crawley, the species having been described from Queensland (Lea, 1923B). Specimens of an unidentified species of *Ataenius*, two at Crawley in December, 1941, and one at Dog Swamp, Tuart Hill in January, 1942, were taken from cow dung. According to Blackburn (1904) the Australian species of *Ataenius* are probably numerous. Considerably more of them came to his notice than all the described

Aphodii of Australia at the time of writing his paper. In view of this statement and the association of species of *Ataenius* with *Aphodius lividus* in other parts of the world (Myers, 1938 ; Lindquist, 1935), the paucity of Ataenii at Crawley is surprising. None were found at Katanning in August, 1941.

Sub-Family **COPRINAE.**

Although they play no part in the succession in cow dung, Coprine dung beetles are of interest because of their habits, which have made them the subject of study from the earliest times. The ancient Egyptians regarded the manipulations of circular dung pellets by *Scarabaeus sacer* as a symbol of the revolution of the planets, and its periodic appearance and disappearance as a sign of eternal life. The Coprinae utilise dung as food for themselves and their larvae without actually living in it. This interesting group is not as well represented in Australia as elsewhere and the species in general are smaller (Lea, 1923A). The chief Western Australian genus is *Onthophagus*, which contains 10 English species found in dung (Stephens, 1839), while Lea (1923A) lists 102 Australian, of which two, *O. nitidor* Blkb. and *O. australis* Guer., frequent carrion at Canberra (Fuller, 1934). One specimen only has been found at Crawley, but *O. ferox* has been taken at Belmont and Claremont, while in the country it occurs at Katanning and at Capel.

Onthophagus ferox digs vertical shafts in close proximity to or under cakes of dung. At about a depth of four inches the direction changes to the horizontal, the resulting passage being about three inches long. In the blind end of this the store of dung is placed. Fresh pig, sheep, cow or horse dung is used and stored in the form of scraps, not moulded into pellets. The excavator of the tunnel is usually found at the bottom of the vertical shaft during the day, the digging apparently being performed at night. There was no indication that the beetles work in pairs as is the case with *Copris lunaris* (Wheeler, 1922). The presence of *Onthophagus* is indicated by piles of turned-up earth round the edges of dung cakes.

F. 11. **ANTHICIDAE.**

In March, 1941, two specimens of *Anthicus hesperi*, King, were collected from cow dung at Crawley. This maintains the relationship between carrion and dung insects, since *A. hoeferi*, Kerg. is a carrion insect at Canberra (Fuller, 1934).

F. 12. **TENEBRIONIDAE.**

Gonocephalum arenarium, Fab. and *Adelium scytallicum*, Pasc., are present at Crawley as shelterers under old, dried fifth stage cow dungs.

Order 6—DIPTERA.

F. 1. **PSYCHODIDAE.**

These tiny moth-like flies are commonly associated with decaying vegetable matter, dung or water. Some species of *Psychoda* breed in drain pipes, the larvae being able to survive hot water and soap (Curran, 1934). The family is widespread. *Pericoma* has been bred from horse and cow dung in Denmark (Thomsen & Hammer, 1936), *Psychoda minuta* from cow dung at Washington (Howard, 1912). Two species of *Psychoda* frequent carrion at Canberra (Fuller, 1934). The economic importance in Australia is negligible apart from occasional nuisance caused by large numbers getting into exposed food material.

At Crawley there appeared to be two species of *Psychoda*, a common grey one and a rarer white. From May to October the larvae, pupae, and adults of grey species occur on and in soft, moist, first to third stage cakes, especially those in the shade. Both larvae (Pl. 1. Fig. 5) and pupae have respiratory siphons which are apparently responsible for the high moisture toleration.

At the time of pupation the larvae come to the surface. The cracks of a cake may be packed tight with the naked pupae. The total time of life history from egg to emergence of adult was 6½ days in September, 1941 (average temperature, 13·9° C.).

The Psychodidae breed in fresher dung than the Sciaridae and consequently precede them in the succession. In the same stage dung as Psychodid larvae and pupae, Sepsid and Drosophilid larva occur, followed later by Cercyon larvae.

F. 2. SCIARIDAE.

Though small flies belonging to *Sciara* sp. infest dung in the laboratory, they are not numerous in the field. The genus *Sciara* is world-wide, having been recorded from North and South America, Africa, Southern Asia, and New Zealand (Skuse, 1889). Tonnoir (1929) estimated the number of described species of *Sciara* and those in collections in Australia, at 63.

They can breed in a wide range of organic materials. Fuller (1934) records them from carrion. The author has bred them from rotting bark and decaying tea leaves. Almost any vegetable detritus which is moist and not exposed to intensities of light or strong air currents seems to suffice. The comparative rarity of these conditions at Crawley accounts for the small numbers of *Sciara* sp. in the field. They breed in late fourth stage dungs more or less sheltered and practically devoid of other insects.

The larvae (Pl, 1, Fig. 6) feed on dung which they comminute into a black powder only held together by moisture. This habit and their large numbers render them a great obstacle to the successful rearing of Scarab larvae in the laboratory. There are indications that they will even attack and consume Scarab pupae.

Pupation occurs in the dung without formation of a pupal cell or cocoon. The pupa has no respiratory processes, though these do occur in some species of *Sciara* (Osten Sacken, 1862). The pupal period varies from two to five days.

Copulation takes place at an early stage, sometimes before the wings of the participants are properly unfolded. The whole life cycle from egg to adult required 10 to 12 days in June (average temperature, 14·5° C.) and July (13·6° C.), 1941. In Denmark, Thomsen and Hammer (1936) estimated the length of the life cycle of a species of *Sciara* to range from 19 to 22 days at temperatures of 19° to 22° C.

The only other Sciarid found at Crawley was a single specimen of ? *Zygoneuro* sp. bred from cow dung in the laboratory in July, 1941.

In spite of their short life cycle and fecundity, the Sciaridae are rendered of minor importance in the succession in cow dung by the frailty of the adults and the restricted physiological requirements of the larvae.

F. 3. SCATOPSIDAE.

These flies are also associated with a variety of decaying materials. *Scatopse* sp. (? *pulicaria*) emerged from vessels containing pig, horse, cow, and calf dung in Denmark (Thomsen & Hammer, 1936), and a species occurs on carrion at Canberra.

At Crawley specimen of ? *Rhegmoclema* sp. emerged in large numbers in the period November, 1940, to April, 1941, from dung brought into the laboratory in November, 1940. In April, 1941, another batch came out of 39-day-old dung which also contained Scarab larvae. They have not been seen in the field and consequently have no place in the succession in cow dung outdoors.

They appear to breed only in late fourth and such fifth stage dungs as remain moist. Both the larva (Pl. 1, Fig. 7) and the pupa (Pl. 1, Fig. 8) show adaptations for living in poorly aerated, moist surrounding. Pupation occurs inside the last larvae skin.

A number of adults dissected in February and March, 1941, contained as many as six to eight nematodes, each in the abdominal region. The parasites must have occupied the greater part of the space of the abdomen.

F. 4. MYCETOPHILIDAE.

A single specimen of ? *Mycetophila* was obtained as a pupa from fifth stage dung in the laboratory. Unlike the Sciarid pupa this was suspended in a diffuse cocoon of white threads. The family is of no importance in the succession.

F. 5. TIPULIDAE.

Two Eriopterine flies were obtained in July, 1941, from artificially-moistened fifth stage cow dung. According to Imms (1938) the larvae may occur in damp situations among grass, roots, decaying vegetation, or may be aquatic. No sign of them in the field was seen.

F. 6. STRATIOMYIDAE.

While the adults of this family are mostly flower feeders, the larvae occur in diverse habitata such as water, soil, and rotting wood (Imms, 1938). The larvae of *Myiochrysa* have been found in cow dung (Williston, 1908). *Actinia incisuralis*, Macq. is found near carrion (Fuller, 1934).

At Crawley, *Neoexaireta spinigera*, Wied. was seen to lay clutches of eggs on fresh cow dung in the laboratory in May and June, 1941. These hatched within three days, but the larvae failed to complete their development. Other larvae collected on 7th November, 1940, which probably belonged to this species, reached the pupal period by 10th April, 1941, but no adults emerged.

Stratiomyid larvae occur occasionally at Crawley in cow dung in the field, although more numerous in rotting vegetation. These larvae, in the course of their relatively long lives, must tolerate the change in condition of the dung from fresh to old and dry, whereas in other dung-breeding insects the larvae are generally restricted to the one stage or to stages which show no marked differences.

F. 7. DOLICHOPODIDAE.

A number of black predaceous flies, near *Asyndetus* sp., occur during autumn and winter on fresh cow dung, preying on the Borborids attracted to it.

F. 8. PHORIDAE.

Flies near *Chaetocnemistoptera* in Curran's Key to the North American genera (Curran, 1934) are frequently attracted to cow dung in the laboratory. The relationship of carrion to cow dung insects holds good as *Sciadocera rufomaculata*, White, and *Beckerina* sp. are members of the carrion association at Canberra (Fuller, 1934).

F. 9. SEPSIDAE.

These are charaeteristic exeremeńt inseets with a world-wide distribution. *Sepsis violacea*, Meigen. breeds almost exclusively in excrement, including that of man (Howard, 1912). There are 30 speeies of Sepsidae in Great Britain (Imms, 1938). In Denmark, numbers of *Sepsis* sp. emerged from cow, horse, and pig dung (Thomsen & Hammer, 1936). Sepsids are eommon in the tropies on dung of all kinds (Patton & Cragg, 1913). In Australia " the known speeies of the family oeeur in the adult stage on garbage, carrion, or vegetation, some being very abundant on flowers. The larvae feed in manure and carrion " (Malloch, 1925A).

At Crawley, Sepsids are the most characteristic flies on cow dung. Two species are present, viz., *Australosepsis fulvescens*, Mall., which appears to contain only males, and its blaek variety *atratula*, Mall., of which both males and females are known, and *Sepsis plebeia*, de Meij. Both species breed in cow dung in the field.

A. fulvescens is most numerous from November to May, and *S. plebeia* during most of the year except January and February. The latter species was collected at Katanning in August, 1941. Both are members of the carrion association at Canberra. A single specimen of *S. hirsuta*, de Meij., was bred from cow dung at Dog Swamp, Tuart Hill, W.A., in January, 1942.

The Sepsids appear on the fresh dung and remain until after the superficial skin has become a firm crust, spending the time in feeding and oviposition. While parading on the dung they generally pair off and indulge in remarkable antics. Each female carries a male, which applies its labella to her cervical membrane and engages its legs on her prothorax. They remain for hours thus, keeping up a ceaseless movement of legs and wings, yet the time of actual sexual contact is short.

Oviposition has been observed only in *Sepsis plebeia*. The female, still carrying the male, partly extrudes the egg several times before depositing it with a sudden thrust of the abdomen. Usually buried in the dung, the egg is occasionally merely dropped on the surface of the cake. Sepsids are frequently seen ovipositing in dung in which eggs of large Muscids have already hatched. This is probably due to the Sepsids remaining for a longer time on the dung, because it is their main food, than do the Muscids, in the diet of which it is only a subsidiary item.

Only one egg is usually laid in a particular spot. Constant returning of the female to the same place results in the formation of large clutches of eggs just below the surfaec with the interlacing respiratory processes (Pl, 1, Fig. 9) forming a white network which is often conspicuous on the surfaec. The eggs hatch in about 24 hours.

The larvae (Pl. 1, Fig. 10) are truly coprophagous, occurring mostly in second and third stage dung, occasionally in the first and very rarely in the fourth. The length of larval life is approximately 10 days.

Pupation normally occurs in the dung itself, usually in the peripheral layers, sometimes on the lower surface. The pupal period in September, 1941 (average temperature, 13 9° C.) was 23 days. The total life history from laying of the egg to emergence of the adult took 33 days in September and October (average temperature, 16·1° C.), 1941.

Because they occur in large numbers and not only consume but tunnel through the dung, the larvae assist greatly in changing its nature. They are parasitised at Crawley by an unidentified *Alysiid* which emerges from the puparium. It is not an efficient parasite as infested stages are not common.

F. 10. **BORBORIDAE.**

Malloch (1925B) mentions the occurrence of larvae and adults of this cosmopolitan family on manure and carrion in New South Wales. Two species of *Leptocera* frequent carrion at Canberra (Fuller, 1934). In America, Howard (1912) reared *Limosina* (= *Leptocera*) and *Sphaerocera* from cow dung and human faeces. In India, *Borborus* is often infected with a herpetomonas as is *Sphaerocera* in France (Patton & Cragg, 1913). Thomsen & Hammer (1936) bred Borborids in cow, calf, pig, and horse dung in Denmark. They were present in large numbers on pig, sheep, and cow dung at Katanning in August, 1941. At Crawley they are associated with carrion, rotting grass, cow, and horse dung.

Most of the small black flies around cow dung at Crawley are Borborids, species of *Leptocera* with a few others belonging to other unidentified Acalyptrate families. The largest species of *Leptocera* has actually been reared from cow dung, though it is the least common in the field. The habits of the pregnant females of the smaller species leave little doubt that they also breed in this medium.

The Borborids are abundant on cow dung from May to October, with a diminution in the complementary period. They rapidly appear on the fresh dung. Unlike the Sepsids they can be found actually underneath the dung pad. The adults feed on the fresh dung, the pregnant females becoming remarkably distended. No information on the immature stages has been gleaned at Crawley.

F. 11. **DROSOPHILIDAE.**

Though the usual association of Drosophilids is with fermentable materials, some breed in cow dung. They are not common at Crawley in the field, being most numerous in July, August, and September, during which period their larvae may be found in second and third stage dungs. The Drosophilids found on cow dung at Crawley and cow and pig dung at Katanning trace to the genus *Cladochaeta* in Curran's Key to the North American Genera.

The larvae are coprophagous and similar in habits to those of Sepsids. Pupation occurs in the drier parts of the dung, the pupal period lasting about three weeks.

F. 12. **OTITIDAE.**

Only two of the species of this family frequenting cow dung at Crawley, *Pogonortalis barbifera* Macq. and *Chrysomyza aenea*, Fab., have been identified. *P. barbifera* resembles the Sepsids in the fanning movements of the wings. That *C. aenea* breeds in cow dung on occasion was shown by examination of a sample of fourth stage cow dung from Armadale in March, 1941. This dung had fermented to the extent that steam rose off it and it felt warm to the touch, both unusual conditions. It contained a large number of puparia and nearly mature larvae of *C. aenea*, pupae of *Cercyon haemorrhoidalis*, one of *Leptaeinus socius*, three larvae of *Saprinus* sp., and a pupa of *Musca domestica*. Specimens in the collection of the Department of Agriculture, Perth, reared from larvae taken in silage waste at Boyanup appear to belong to *C. aenea*.

The larvae perform peculiar skipping evolutions when disturbed. The body is flexed ventrally to enable the mouth hooks (Pl. 1, Fig. 11) to grasp the terminal part of the body, probably the raised area round the anus. Then the longitudinal body muscles are strongly contracted. The mouth hooks suddenly release their hold, producing sufficient force to flip the

larvae up to a foot from its starting point. These acrobatics are similar to those performed by the larvae of *Piophila casei*, the so-called "Cheese Skippers." Continuous stimulation will cause a larva to repeat these movements until it can no longer lift itself from the ground.

Pupation occurs in the dung, the puparium being reddish-brown in colour. No exact figures of the length of life history are available. Larvae of unknown age collected on 3rd April, 1941, had all given rise to adult flies by 30th May, so that in some cases the life history requires more than 58 days, longer than that of dung-breeding Muscids.

F. 13. CALLIPHORIDAE.

Sub-Family 1: CALLIPHORINAE.

Calliphora (*Neopollenia*) *australis*, Boisd., *Calliphora* (*Procckon*) *nociva*, Hardy, and *Lucilia cuprina*, Wied., all visit fresh cow dung in spring and autumn, though never in large numbers. Attracted by the odour, the adults suck up the liquid dung, often in large quantities, but no evidence of their breeding in cow dung at Crawley was obtained. Their association with it is thus of a casual nature and can have no effect on the succession.

Sub-Family 2: SARCOPHAGINAE.

In the period October-November, 1941, 10 specimens of *Sarcophaga* (*Parasarcophaga*) *depressa*, Desvoidy, were reared in cow dung from Crawley, and in January, 1942, 53 from dung obtained at Dog Swamp, W.A. The eggs are deposited in fresh dung, especially in strong-smelling cakes. In spite of their large size, 20 to 30 larvae per cake may occur. They generally leave the dung to pupate without displaying the same degree of restlessness prior to pupation displayed by the larvae of *Calliphora stygia*. The cakes which sheltered the larvae contained normal populations of other insects.

S. varia Walk. normally breeds in cow dung in New Zealand. Two species of *Sarcophaga* frequent carrion at Canberra (Fuller, 1934), while various species of the genus attack living sheep as secondary blowflies in the tropical and sub-tropical parts of Northern Australia (C.S.I.R., 1933).

F. 14. MUSCIDAE.

Sub-Family 1: FANNIINAE.

? Fannia sp.

One fly probably belonging to this genus was bred from cow dung in the laboratory at Crawley. The eggs were laid on 16th September, 1941, hatching about eight days later into "hairy" maggots. These remained on the surface of the dung without penetrating it until 20th October, when four pupated. The only fly which emerged at all did so on 2nd November.

In the field, eggs are common and larvae have been seen on two occasions, having actually penetrated into third stage dung but no adults have been bred out.

Sub-Family 2: MUSCINAE.

Musca domestica, Linn.

Cow dung has very little attraction for the ovipositing female and this fly has not been bred out of it at Crawley. A single puparium, which subsequently gave rise to a female *Musca domestica*, was found in cow dung from Armadale which was of an unusual type, as described in the section on the Otitidae, though it contained the usual insect population. The presence of the puparium is remarkable, because the dung contained no admixture of any

other material. Where *M. domestica* is found breeding in cow dung, the material is generally mixed with straw or some such substance (Austen, 1928. Results quoted by Thomsen & Hammer).

Musca vetustissima, Walker.

This is the common bush fly which annoys workers in the open because of its habit of clustering on the face and attacking the eyes. Its activities have earned it the title of the " Queensland cattle fly " and it also pesters horses. It is of some economic importance because it transmits *Habronema muscae*, a Nematode parasite in the stomach of the horse and another undetermined species of *Habronema* which causes habronemic conjunctivitis of horses (Johnston & Bancroft, 1920). It is probably capable of setting up Anthrax infection under some circumstances (Cleland, 1913). The life history has been described by Johnston & Bancroft (1919), the breeding medium being either horse or cow dung. The total period of development from the egg to the adult in the Eidsvald district of Queensland was found to be 10 to 14 days in November.

At Crawley the flies are numerous on fresh dungs although only six specimens have actually been reared from dung in May, 1941. In January, 1942, large numbers were reared from cow dung from Dog Swamp, Tuart Hill— W.A., which also contained maggots of *Sarcophaga* (*Parasarcophaga*) *depressa*, Desvoidy.

Sub-Family 3 : **ANTHOMYIINAE.**

Hylemyia deceptiva, Mall.

A single specimen of this species or near to it was bred out from cow dung in September, 1941. *H. deceptiva* is recorded on carrion at Canberra (Fuller, 1934). Another undetermined species of *Hylemyia* was bred from second stage cow dung in June, 1941.

H. variata Fallen and *H. strigosa* Fallen, which occur in Ayrshire and Arran in West Scotland are ovoviviparous flies. Whether this is the case with the local species is as yet unknown.

Sub-Family 4 : **PHAONIINAE.**

Rhynchomydaea (Hardyia) carinata, Stein.

Flies near this species are the commonest of the large Muscids frequenting cow dung at Crawley. The adults, which feed on fresh dung, occur during the period May to November, while specimens have been bred out from cow dung in the period March to November. The species is present at Katanning.

Eggs are laid singly with the anterior ends projecting in fresh dung. About 14 larvae is the maximum number which mature in each cake. They occur in first to third stage dung, the larvae period being about 14 days. The larvae are coprophagus.

Pupation occurs in the dung, usually in a hollowed cavity on the lower or near the upper surface. Sometimes, after heavy rain, puparia may be found on top of cakes in shaded situations. The pupal stage lasts about three weeks. The total cycle from egg to emergence of the adult took 34 days in September (average temperature 13·9° C.) and October (16·1° C.), 1941.

HELINA.

This genus is wide-spread in Australia (Malloch, 1925C) and is represented at Crawley by the following species :—

Helina coerulescens, Stein.

Though common on fresh dung at Crawley during the same period, this metallic fly has not yet been reared from cow dung. It is similar in habits to *R. carinata.*

Helina hypopleuralis, Mall.

Four specimens bred from cow dung at Crawley in September and November, 1941, belong to this species or to one near it.

Helina regina, Mall.

One specimen near this species was reared from cow dung at Crawley.

Muscina stabulans, Meig.

This wide-spread species has a variety of breeding media. Howard (1912), in America, lists as food for its larvae, decaying animal matter, cow dung, fungi, caterpillars, larval bees, dead pupae, decaying plant materials, and human excreta. Fuller (1934) notes its association with carrion. In Denmark it was reared from pig, cow, and calf dung (Thomsen & Hammer, 1936). The flies have been reared from rotting potatoes and also from carrion in Australia (Hardy, 1938), whereas Muirhead Thomson (1937) stated that he had never seen nor had been able to induce oviposition by *M. stabulans* on carrion.

Only one specimen has been reared from cow dung at Crawley.

Order 7—HYMENOPTERA.

F. 1. ALYSIIDAE.

An undetermined species of *Alysiid* is associated with cow dung at Crawley, most numerous during the period February to November. In spite of their delicate build they sometimes penetrate deeply into the interior of cakes, presumably to parasitise Sepsid and Drosophilid larvae, since puparia so infested are occasionally found. Fenales are more numerous than males.

An Alysiid, *Alysia manducator* Pantzer, has been introduced into Australia as a parasite of sheep blowflies, but it has failed to establish itself (C.S.I.R. 1933).

F. 2. FIGITIDAE.

Small wasps belonging to this family are encountered throughout the year in and on first stage dungs. As no material parasitised by them was obtained, their hosts are not known. This is also true of a number of other wasps belonging to various families, which were not identified because nothing is known of their habits.

F. 3. FORMICIDAE.

On fresh dungs, small ants are usually present as predators attacking adult Borborids and Sepsids. In due course they carry off immature stages of beetles and flies. They are most active during the summer, at which time they appear to influence the population considerably. Nevertheless, in August, 1941, many of the second and third stage cow dungs were packed with pupae which ants were removing.

Small amber-coloured ants frequently form colonies under dung cakes of all stages in spite of the conclusions of Forel and Wheeler that they will not do so except to seek shelter from the sun or moisture, both of which are amply available at Crawley under stones or vegetation. Again, the odour does not prevent ants from penetrating into even fresh dung, although Wheeler (1926) refers to their dislike of bad odours such as those of carrion and mammalian faeces.

Order 8—LEPIDOPTERA.

Three larvae collected on the 5th September, 1941, on top of late fifth stage cow dung about three months old, kept in the laboratory. They were apparently feeding on the dry and crumbling fibres of the cake. The three larvae pupated five days later. After an additional 23 days, one gave rise to a small Oecophorid moth. The larvae have not been seen in the field.

The association of these larvae with cow dung is of the same order as *Monopsis rusticella*, Hubn., a Tineid moth breeding in the wool of an old sheep carcase reported by Fuller (1934), being divorced in time and space from those insects which form the succession proper.

8. OTHER ANIMALS ASSOCIATED WITH COW DUNG AT CRAWLEY.

A. Other ARTHROPODA.

1. ACARINA.

A large number of mites belonging to the Parasitidae are found in cow dung at Crawley. They breed in the dung and frequent all stages except the final part of the fifth. A considerable variation in the mite population of individual cakes is noticeable.

In the field both flies and beetles are found carrying numbers of mites which may merely hang by their claws or adhere by a secretion. *Proctophanes sculptus*, Hope, is especially liable to act as a carrier, as its clumsy build and slowness of movement prevent it from dislodging its passengers.

Under laboratory conditions, where dung is kept covered, mites multiply to a remarkable extent. Though mites have not been seen, except in a few doubtful cases, to molest them, immature stages of flies and beetles diminish in number in dungs with a high Acarine population density.

At Katanning in August, 1941, no Parasitids were seen on cow dung in the town itself and very few in material five miles away, a strong contrast to the large numbers present at Crawley in the same month.

2. CRUSTACEA.

Fourth and fairly moist fifth stage cow dung often shelters associations of *Porcellio* sp. at Crawley. They offer little or no competition to such immature stages of Hydrophilids or Scarabaeids as are present.

B. NEMATODA.

If kept in closed vessels, cow dung is an ideal nidus for these minute worms. In the field they are not noticeable as a rule until pupae of *Cercyon* begin to appear in fourth stage dung cakes. A number of these have bunches of Nematodes hanging from the appendages or on the ventral body surface, often numerous enough to force the wings of the pupa into an unnatural posi-

tion almost at right angles to the long axis of the body. Since most of the pupae in this condition are able to transform normally, it seems that the Nematodes are free living forms attracted to them by the moisture given off.

Adult Cercyons, when kept in closed vessels with cow dung, often contain Nematodes in the posterior part of the alimentary canal and genital tract as well as on the moist body surfaces. There is no reason to believe that the presence inside the body is due to anything more than the tendency to migrate into any aperture.

C. ANNELIDA.

Fresh cow dung attracts earthworms which will consume large quantities if it is applied to garden beds containing them. They are also of frequent occurrence in heaps of fourth stage cow dung which has retained moisture. Nothing definite is known of the degree of competition they offer to the true dung insects.

9. FEATURES OF THE SUCCESSION IN COW DUNG.

Having referred to various aspects of the biology of the insects concerned, it is now possible to draw up a scheme showing the features of the succession, defined according to the stage through which the cow dung passes, as set out in section 4.

First Stage.

This is characterised by the activities of dung insects on the surface of the fresh dung. The Sepsids, Borborids, Calliphorids, Otitids, and Muscids appear to feed on the liquid dung in such a haphazard manner that the order varies for practically every dung.

The dung beetles are also prompt in arrival and again no particular order can be defined. The Staphylinids, Hydrophilids, Histerids (in season) and Aphodiines, except *A. ambiguus*, all commence to penetrate either through natural crevices on both surfaces or by creating apertures in the superficial skin.

Toward the end of the first stage, the number of flies diminishes. The Calliphorids leave first, the only attraction for them being the soft dung now covered with a firm skin, and then the large dung-breeding Muscids after oviposition. The Sepsids and Borborids remain longer, and the former may be seen ovipositing over some days. The predatory Dolichopodids and *Creophilus erythrocephalus* also leave when the numbers of their prey diminishes.

Second Stage.

The surface layers of the cake become penetrated by the dung beetles. Sepsids and Borborids are still present. Mites and Collembola appear early in this or late in the first stage. Although the eggs of Muscids and Sepsids have hatched, the small size of the larvae renders them inconspicuous. Adult Psychodids are to be found ovipositing on cakes in the shade.

Third Stage.

The dung is extensively penetrated by beetles. In many cases an unpenetrated core near the lower surface is left but many cakes are completely riddled. The activities of Cercyons and *Aphodius lividus*, by admitting air into the dung, give it its characteristic black colour. The latter part of this period is primarily one of immature stages. The population of Sepsid, Drosophilid, and Psychodid larvae becomes very high. Cercyon and even occasional Scarab larvae appear towards its end, as the emigration of adult beetles begins.

Fourth Stage.

Except for occasional specimens, usually Staphylinids, the population of adult beetles is low apart from *Aphodius ambiguus*. Larvae and pupae of Staphylinids, Cercyons, eggs and larvae of Aphodiines are present in the peripheral regions. The Psychodids have disappeared. Larvae of *Sciara* sp. hatch out in this stage. Most of the Brachycerous Dipteran larvae have pupated. Mites and Collembola still remain in some numbers.

Fifth Stage.

The population is essentially similar to that of the previous stage, progressively diminishing in size as the dung becomes drier. Ultimately, in the final stages, the Aphodiine larvae have undergone metamorphosis and vanished. The dung no longer contains insects and serves only to shelter a few, the presence of which under it is purely fortuitous.

The following minor successions compose the main one :—

1. The succession of visitors to inhabitants, which arises out of the alteration of the dung, due more to oxidation and other chemical changes at its surface than to any activities of the insects.
2. The succession among the adult Coleoptera. The majority of the early invaders move out in the third stage and are succeeded by *Aphodius ambiguus* in the early fourth, which is replaced in turn only by the casual shelterers of the fifth. The cause of the emigration in the third stage is not always clear. High population densities may cause a rapid change in the quality of the dung which becomes unsuitable for the adults and consequently they leave. There are, however, many instances in which the insects abandon the dung while it still offers abundant food and space. Competition may cause the emigration of surplus individuals. This would lessen its intensity and there would be no reason for any more to leave. The exodus of all beetles from a dung of this type may be due to the tendencies found among gregarious insects to keep close together and to imitate each other's movements, which are believed to be responsible for such phenomena as the swarming of locusts (Uvarov, 1928). It is an open question whether the gregariousness of dung beetles is real or due to purely chance associations resulting from large numbers of individuals responding to the same stimulus. In any case, the migration of dung beetles is a gradual process not comparable with any form of swarming.
3. The succession among the larval stages. Larvae appear in cow dung in the following order :—

   1st Stage—Sepsid, Drosophilid, Borborid (?), Muscid.
   2nd Stage—Psychodid.
   3rd Stage—Hydrophilid, Staphylinid.
   4th Stage—Aphodiine, Sciarid.

In carrion the succession is assisted by the predaceous activities of the secondary blowfly maggots which actually attack or drive off those of the primaries. In the cow dung population none of the larvae of importance in the succession are predatory on the others except those of Staphylinids, which do not appear in sufficient numbers to influence the total. Aphodiine larvae succeed those of *Cercyon* only because their physiology is better adapted to existence in fourth stage dung. The effect of competition is therefore to regulate the number of individuals found in any stage and plays little part in replacing one species by another.

Chapman (1931) divides animal successions into passive and active according to the part played by the animals concerned. Though less so than that in carrion, the succession in cow dung is of the active type since the insects do affect their environment. Volume for volume cow dung supports a smaller population than carrion. This is due to the less powerful odour which is the primary attracting stimulus, the less nutritious nature of the dung itself, and in the case of flies the comparatively short time during which it is a suitable medium for oviposition owing to the early formation of a more or less impervious crust. All these factors result in a less well-defined succession than occurs in carrion.

As has been indicated previously, there is a correlation between the type of insect in carrion and that in dung, many species being common to both habitats. Nevertheless, each substance has its own characteristic insects physiologically adapted to it with only a casual association with the other. Blowflies visit cow dung but their life history is bound up with carrion. In the same way, Cercyons are sometimes found on carrion yet they are characteristic cow dung insects.

Both in carrion and cow dung are insects which either have a wide distribution themselves, *e.g.*, *Aphodius lividus*, *Cercyon haemorrhoidalis*, or have closely allied species in other parts of the world, *e.g.*, *Sepsis plebeia* This is to be expected, as neither carrion nor faecal matter is subject to geographical variation.

10. THE ECONOMIC IMPORTANCE OF INSECTS FOUND IN COW DUNG.

The primary sheep blowflies *Calliphora australis* Boisd, *C. nociva* Hardy, and *Lucilia cuprina* Wied., have only a casual association with various species of *Sarcophaga*, are secondary sheep blowflies, and some of these breed in cow dung, though the importance of this material to the flies as a breeding substance is not known. *Musca domestica* Linn. prefers other breeding nidi, and no evidence has been seen that *Stomoxys calcitrans* Linn., which occurs in numbers in Perth, ever frequents dung at Crawley. Research in various parts of the world has shown that cow dung is among the least favoured of the breeding media of this fly.

Musca vetustissima Walker is a common pest in Perth on man and cattle. Cow dung is an important source of the fly here, especially that dropped in swampy situations. *Rhynchomydaea carinata* Stein and the species of *Helina* associated with cow dung at Crawley are not domestic insects, nor have they, as far as is known, any habits rendering them objectionable to man. *Muscina stabulans* Fallen is not abundant at Crawley. In any event, cow dung is only one of a large number of breeding materials utilised by this fly.

In South Australia and Tasmania, two Aphodiines, which normally feed on dung, have come under notice because their lavae have been found damaging pastures and lawns (Swan, 1934; Evans, 1941). These are *Aphodius howitti*, Hope, and *A. tasmaniae*, Hope, neither of which has been collected at Crawley. No complaints have been received by the Department of Agriculture against any local species in this connection.

When L. J. Newman, in 1929, succeeded in rearing *Lyperosia exigua* de Meij., the Buffalo fly on cow dung under midwinter conditions in Perth, without the application of artificial heat, it was feared that this pest might be introduced in the dairying regions in the southern part of the State. Precautions against this possibility in the form of spraying cattle before they left North-West ports were introduced (Toop, 1931). The fly has not been reported in the South-West, nor has any sign of it been seen at Crawley.

The typical dung insects—Sepsids, Hydrophilids, Aphodiines, etc., all play their part as seavengers in getting rid of waste material, but the actual evaluation of the economic importance of this part is practically impossible.

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EXPLANATION OF PLATE 1.

Fig. 1.—*Cercyon haemorrhoidalis* Fab. Variety 1.
Ventral view of Adult.

Fig. 2.—*Cercyon haemorrhoidalis* Fab.
Dorsal view of Mature Larva.

Fig. 3.—*Leptacinus socius* Fauv.
Lateral view of Pupa.

Fig. 4.—*Aphodius lividus* Oliv.
Ventral view of Pupa.

Fig. 5.—*Psychoda* sp.
Ventral view of Larva.

Fig. 6.—*Sciara* sp.
Partially dorsal view of Larva.

Fig. 7.—? *Rhegmoclema* sp.
Lateral view of Larva.

Fig. 8.—? *Rhegmoclema* sp.
Lateral view of Pupa extracted from skin of last larval instar.

Fig. 9.—*Sepsis plebeia*, de Meij.
Egg.

Fig. 10.—*Sepsis plebeia*, de Meij.
Lateral view of terminal segments of Larva.

Fig. 11.—*Chrysomyza aenea* Fab.
Lateral view of anterior region of nearly mature Maggot.

Fig. 12.—*Rhynchomydaea* (Hardyia) *carinata* Stein or near.
Posterior spiracles of seeond Larva.

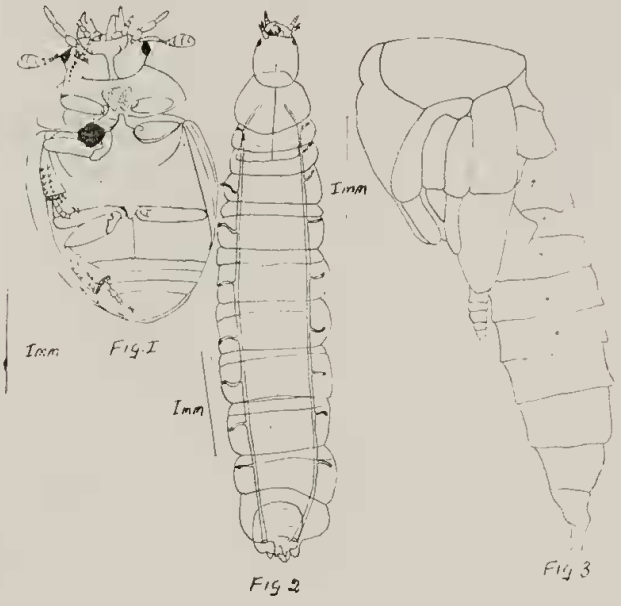

Fig. 1 Fig. 2 Fig. 3

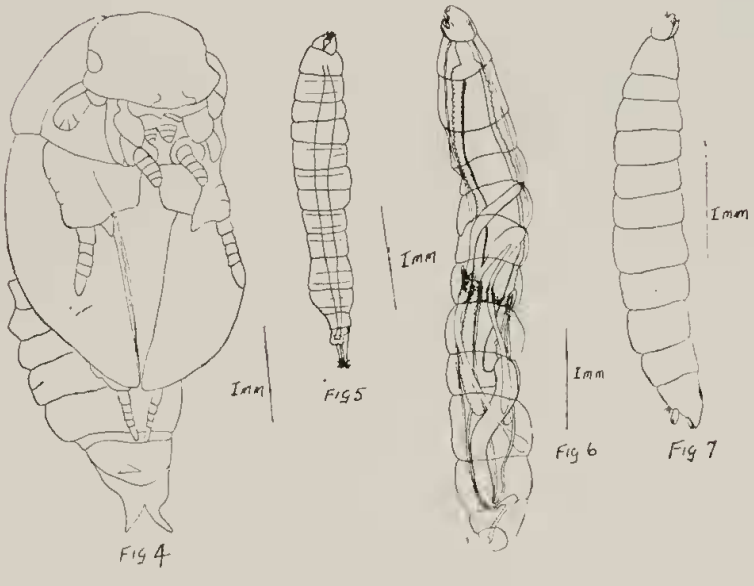

Fig. 4 Fig. 5 Fig. 6 Fig. 7

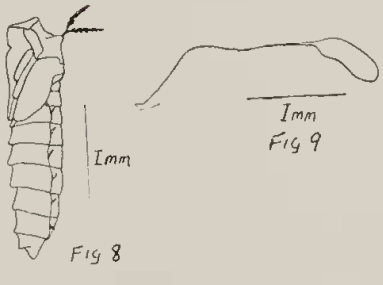

Fig. 8 Fig. 9

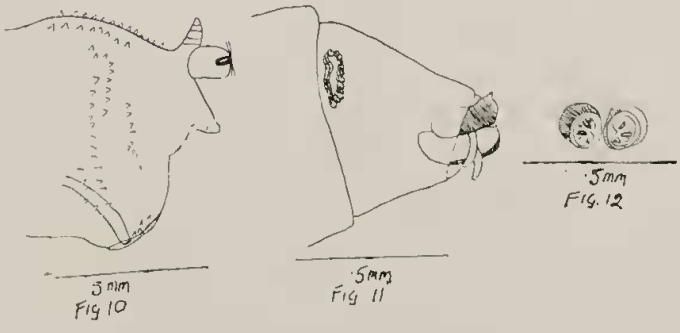

Fig. 10 Fig. 11 Fig. 12